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Desert vegetation distribution and species-environment relationships in an oasis-desert ecotone of northwestern China

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Abstract: Environmental heterogeneity significantly affects the structure of ecological communities. Exploring vegetation distribution and its relationship with environmental factors is essential to understanding the abiotic mechanism(s) driving vegetation succession, especially in the ecologically fragile areas. In this study, based on the quantitative analysis of plant community and environmental factors in 68 plots at 10 different transects in the Minqin oasis-desert ecotone (ODE) of northwestern China, we investigated desert vegetation distribution and species-environment relationships using multivariate analysis. Two-way indicator species analysis (TWINSPAN), detrended correspondence analysis (DCA), and canonical correspondence analysis (CCA) methods were used. A total of 28 species, belonging to 27 genera in 8 families, were identified. Chenopodiaceae, Zygophyllaceae, Gramineae, and Leguminosae were the largest families. Annual and perennial herbs accounted for 28.60% of the total number of plants, while shrubs (42.90%) were the most dominant. *Nitraria tangutorum* was the constructive species of the desert plant community. We divided the 68 plots surveyed in this study into 7 community types, according to the results of TWINSPAN. The distribution of these 7 communities in the DCA ordination graph showed that species with a similar ecotype were clustered together. Results of CCA indicated that groundwater was the dominant factor influencing vegetation distribution, while distance between plot and oasis (Dis) and soil electrical conductivity (EC) were the local second-order factors. Our study suggests that optimizing the utilization of groundwater in oases is key to controlling the degradation of desert vegetation. The favorable topographic conditions of sand dunes should be fully utilized for vegetal dune stabilization, and the influence of soil salinity on the selection of afforestation tree species should be considered.

Keywords: TWINSPAN classification; ordination; desert plant; groundwater; oasis-desert ecotone; species-environment relationship; Minqin

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1 Introduction

A central issue in community ecology is to understand the environmental factors that regulate species distribution and plant community diversity (Ohmann and Spies, 1998). It is now recognized that environmental heterogeneity significantly affects the structure of ecological communities (Vivian-Smith, 1997). Species composition is one of the important attributes of plant community structure and is primarily restricted by environmental factors, including climate, elevation, biotic factors, groundwater, and soil properties. These factors influence vegetation patterns variably at different spatial and temporal scales. Climatic factors control the distribution of vegetation on a large scale, while edaphic factors are more important on a small scale (Siefert et al., 2012). Compared with humid areas, plants in arid and semi-arid regions are more susceptible to environmental factors (Böer and Sargeant, 1998). Groundwater is the main source of moisture for perennials in arid and semi-arid regions, ensuring their long-term survival (Thomas et al., 2006). It also affects species distribution, community characteristics (Xu et al., 2007; Li et al., 2010), and plant zonation (Cooper et al., 2006; Rzepecki et al., 2011) by driving water availability (Liu et al., 2017). Precipitation patterns influence the aboveground net primary production of sand-fixing vegetation (Li and Zhao, 2017), community structure (Cheng et al., 2006), annual plant phenology (Huang et al., 2018), photosynthesis (Liu et al., 2012), and carbon cycle (Thomey et al., 2011). Dune mobility affects the settlement and expansion of desert plants (Hernández-Cordero et al., 2015). Soil salinity, sodicity, and texture are the main factors affecting vegetation distribution in Mediterranean saltmarshes (Moreno et al., 2018). Soil total phosphorus and sand are the dominant factors influencing distribution patterns of desert plants in the Heihe River Basin (Li et al., 2018). Therefore, groundwater, climate, microtopography, and edaphic factors are strong driving forces that sustain ecosystem functions, particularly in arid desert regions (Sommer and Froend, 2014; An et al., 2015; El-Keblawy et al., 2015). Understanding the species distribution and its relationship with environmental factors in arid desert regions will help in planning, managing, and restoring the desert ecosystems.

The oasis-desert ecotone (ODE) is a typical landscape located downstream of inland rivers in arid regions and is influenced by the interaction between the expanding oasis and encroaching desert. It is a key ecological barrier that protects oasis from the hazards of sand storms (Zhang et al., 2017) and is sensitive to human activities and climate changes. Therefore, the ODE is characterized by environmental vulnerability (Pi et al., 2017). The Minqin ODE in northwestern China is an important ecological barrier that prevents the closing of Badain Jaran Desert and Tengger Desert (Wang and Cui, 2004). Increase in farm irrigation since the late 1950s in the Minqin oasis has caused a dramatic decline in the groundwater level (Zhang et al., 2012). Because of prolonged drought, dominant species such as *Tamarix chinensis*, *Haloxylon ammodendron*, and *Nitraria tangutorum* have been degraded in the Minqin ODE (Ma et al., 2007, 2009; Wang et al., 2015; Ji et al., 2016), thus posing a serious threat to the stability of oases. Therefore, controlling further degradation of desert plants in this region is crucial.

Relationships between desert plants and environmental factors in the Minqin ODE have been extensively investigated. These studies revealed the following aspects: (1) the effects of *H. ammodendron* plantations on soil physical-chemical properties, soil microorganisms (Xi et al., 2015; Fan et al., 2016), spatial pattern, soil water, and water budget of *N. tangutorum* nebkhas (Qiu et al., 2015; Wang et al., 2015; Yang et al., 2015); (2) the relationships of climate changes with vegetation gradient characteristics, vegetation restoration, water use, and reproductive phenology (Du et al., 2010, 2011; Ma et al., 2010; Chang et al., 2012; Zhu et al., 2013; Han et al., 2015); (3) the clonal population of *Calligonum mongolicum* and its relationship with environmental factors (Zhou et al., 2012); and (4) vegetation succession, niche, traits, and physiological responses of desert plants to groundwater (Peng et al., 2004; Yang et al., 2007; Shi et al., 2008; Wei et al., 2008), vegetation, and soil nutrients (Chen et al., 2007, 2009). However, most of these studies investigated the relationships between individual environmental factors and plants on a relatively small scale. Research on the combined effects of climate, soil, microtopography, and groundwater on the species composition and vegetation distribution of desert communities using multivariate analysis

has not been reported. Understanding vegetation distribution and its relationship with environmental factors is an important prerequisite for the restoration and reconstruction of desert communities in the Minqin ODE.

This study investigated the percentage variation in species composition of desert plants explained by climate, groundwater, topography, and soil over an area of 2200 km^2. The main object of this study was to quantify the influence of environmental factors on species composition of sand-fixing plants in the Minqin ODE.

2 Materials and methods

2.1 Study area

The study area is located in an ecotone (38°34′58″–39°06′21″N, 102°55′14″–103°37′22″E; 1294–1411 m a.s.l.; Fig. 1) between the Minqin oasis and the southwest fringe of the Badain Jaran Desert in northwestern China. The area is characterized by a typical temperate desert climate, with annual mean air temperature, mean annual precipitation, and mean annual evaporation of 7.7°C, 115.8 mm, and 2664.0 mm, respectively. Precipitation mainly occurs from July to October, and snowfall is sporadic in winter. The annual mean wind velocity is 2.5 m/s, and the prevailing wind comes from northwest. The average annual duration of gales, sandstorms, and blowing sand during 1959–2015 was 26.3, 25.0, and 37.5 d, respectively. The Minqin is one of the important sources of dust in China, resulting from its fragile eco-environment (Dong et al., 2010). The main soil types are chestnut, brown, and aeolian sand. The zonal vegetation in the region is described as desert steppe. Typical local shrub species include *N. tangutorum*, *Tamarix ramosissima*, and *C. mongolicum*, whereas *H. ammodendron* is the dominant artificial species. Over reclamation and overexploitation of groundwater are the main human activities that indirectly affect the desert vegetation distribution.
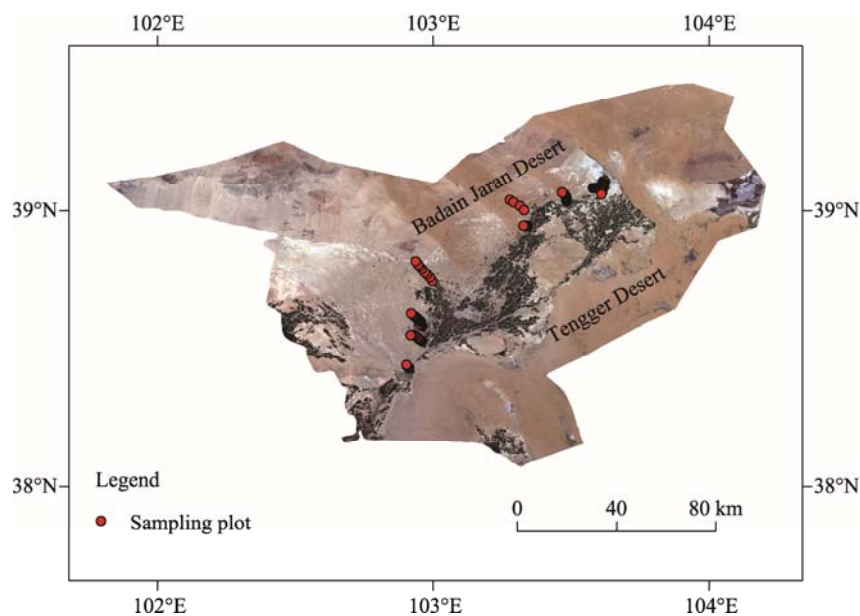

Fig. 1 Location of the study area and sampling plots

2.2 Experimental design and data collection

The type of vegetation was investigated during the rainy seasons (July to September) from 2012 to 2015. Ten oasis-desert transects were selected to explore the quantitative relationships between environmental factors and plant species along a groundwater gradient from Baqu to Huqu (Chen and Feng, 2013). A total of 68 plots, spaced 500 m apart each other, were established at the 10 different oasis-desert transects (Fig. 1). The distance between plot and oasis (Dis) was recorded.

Each plot was divided into 3 shrub quadrats (10 m×10 m) spaced 30 m apart, and 3 herb quadrats (1 m×1 m) were established on the diagonal of each shrub quadrat. In each quadrat, the species name, height, abundance, and crown diameter were recorded. In addition, the longitude, latitude, and elevation of each quadrat were determined using the global positioning system (GPS; Etrex, Garmin Ltd., Olathe, KS, USA). We estimated species cover according to the Braun-Blanquet cover-abundance scale (Mueller-Dumbois and Ellenberg, 1974). The height, density, frequency, and cover of each species in all shrub and herb quadrats of each plot were averaged and then transformed into the relative values. The average importance value (IV) of each species was calculated according to Equation 1 (Curtis and McIntosh, 1951):

$$IV = RA + RD + RF ,$$ (1)

where RA, RD, and RF represent the relative abundance, relative dominance, and relative frequency of the species, respectively.

Dominance index was calculated using Equation 2 described below (Simpson, 1949).

$$C = \sum_{i=1}^{s} \left(\frac{n_i}{N} \right)^2 ,$$ (2)

where C is the Simpson dominance index; S is the total number of species in the plot; n_i represents the importance value of species i; and N is the sum of importance value of all species in the plot.

Shannon-Wiener diversity index, Pielou evenness index and Margalef richness index were respectively calculated according to Equations 3–5 as follows (Mueller-Dumbois and Ellenberg, 1974):

$$H' = -\sum P_i \ln P_i ,$$ (3)

$$J_{sw} = H'/\ln S ,$$ (4)

$$D = (S-1)/\ln N ,$$ (5)

where H' is the Shannon-Wiener diversity index; P_i is the relative importance value of species i; J_{sw} is the Pielou evenness index; S is the total number of species in the plot; D is the Margalef richness index; and N is the sum of importance value of all species in the plot.

Approximately 500 g of soil was randomly sampled from depths of 0–5, 5–20, 20–40, 40–60, 60–80, 80–100 cm in each plot. Soil samples were replicated three times at different soil depths. These samples were dried and sieved through a 2-mm mesh to remove debris and stones. The sand (0.020–2.000 mm), silt (0.002–0.020 mm), and clay (<0.002 mm) compositions were measured using a laser particle size analyzer (Malvern Mastersizer 2000, Malvern, England). Soil water content (SWC) was measured by drying soil samples in an oven at 105°C for 24 h. Soil organic matter (SOM) content was determined by the oxidation of soil samples with potassium dichromate in a sulfuric acid environment, according to Anne's method (Grubb, 1977). Total nitrogen (TN) content was measured using an Autokjeldahl Unit (Segundo et al., 1992). Available phosphorus (AP) content was measured using the Bray method (ISSCAS, 1978). Soil electrical conductivity (EC) and pH were determined using a portable conductivity meter (Cole-Parmer Instrument Company) and the potentiometric method, respectively.

Data on 96 monitoring groundwater wells in the Minqin oasis were obtained from the Wuwei Water Affairs Bureau. Then, the depth of groundwater (Dep) in each plot was calculated using the Kriging interpolation method (Chen et al., 2012). Data of mean annual precipitation (Pre) and annual mean temperature (Tem) were derived from the CRU Global monthly precipitation and temperature data sets (resolution of 0.5°×0.5°), which were downloaded from the National Earth System Science Data Sharing Infrastructure, National Science & Technology Infrastructure of China.

2.3 Statistical analysis

We classified the plant community by two-way indicator species analysis (TWINSPAN) using WinTWINS version 2.3, according to the importance value of plant species. Detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) were performed

using CANOCO version 5.0 software for Windows (Microcomputer Power, Ithaca, NY, USA) to determine the species-environment relationships. Specifically, DCA was used to reveal the gradient of species distribution, and CCA was carried out to explore the relationships between species distribution and environmental factors. Fourteen environmental factors were contained in the environment matrix to perform the CCA, including the Dep, Dis, altitude, Pre, Tem, SWC, sand, silt, clay, TN, AP, SOM, EC, and pH. All environmental factors were standardized or normalized by log (y+1) to ensure the homogeneity of variance, and rare species were eliminated (Lepš and Šmilauer, 2014). Differences in environmental factors and diversity indices among different communities were explored by variance analysis (ANOVA) and Duncan's multiple range test in SPSS version 18.0. Difference was considered as significant at P<0.05 level.

3 Results

3.1 Composition of vegetation

Field surveys recorded a total of 28 species (24 dicot and 4 monocot species) belonging to 27 genera in 8 families in the study area. Annual and perennial herbs accounted for 28.60% of the total number of plants, whereas shrubs occupied 42.90% and were the most dominant. Chenopodiaceae, Zygophyllaceae, Gramineae, and Leguminosae were the largest families, comprising 25.00% (7 species), 17.86% (5 species), 14.29% (4 species), and 14.29% (4 species) of the total number of recorded species, respectively. The Simpson dominance index values of species were as follows (arranged in decreasing order): *N. tangutorum* (4.726), *H. ammodendron* (2.055), *Agriophyllum squarrosum* (0.862), *C. mongolicum* (0.783), and *Phragmites australis* (0.739) (Table S1).

3.2 Classification of vegetation

We identified 7 ecologically distinct plant communities based on the third level division in TWINSPAN classification (Fig. 2). Since vegetation distribution is a continuum, similar species exist among different community types, which reflect the transitional characteristic of vegetation distribution. Due to variance of environmental conditions, significant differences were observed in the diversity indices of the 7 communities. Typical fruticous desert community (Group 1) was dominated by the shrub *N. tangutorum* located close to the desert. Desert shrub community (Group 2) was dominated by the shrub *C. mongolicum* and herb *A. squarrosum*, mainly in the area of mobile sand dunes. *Artemisia* desert community (Group 3) was dominated by *Artemisia salsoloides*, mainly in the area of semi-fixed sand dunes. Dwarf tree desert community (Group 4) was dominated by *H. ammodendron*, which was mostly distributed at the edge of the oasis, accounting for 51.5% of the total area of artificial sand-fixing forest. Halophyte bush vegetation community (Group 5) was dominated by *T. ramosissima* and *Reaumuria songarica*. Salt semi-shrub community (Group 6) was dominated by *Kalidium foliatum* and *Lycium ruthenicum*, mainly in the area of salinized low sandy land or hilly lowland of the Qingtu Lake. Saline meadow community (Group 7) was dominated by *P. australis*, mainly in the area of artificial water injection zone of the Qingtu Lake. The results of TWINSPAN classification reflect the ecotypes of different communities (Table 1; Table S2).

3.3 Species-environment relationships

The DCA was used to measure the variation in community structure with environmental gradients, providing a gradient length reference for community ordination. The cluster types obtained by TWINSPAN classification were consistent with the results of DCA ordination in the study area (Fig. 3). According to the DCA results, the 7 community types were identified as follows: Group 1, *N. tangutorum-P. australis+A. squarrosum*; Group 2, *C. mongolicum+H. ammodendron-A. squarrosum*; Group 3, *N. tangutorum+H. ammodendron+A. salsoloides*; Group 4, *H. ammodendron+N. tangutorum+Limonium aureum*; Group 5, *N. tangutorum+R. songarica+T. ramosissima*; Group 6, *K. foliatum+N. tangutorum+L. ruthenicum*; and Group 7, *N. tangutorum-P. australis-Salsola collina*.

According to Pearson's correlation analysis, most environmental factors showed strong

correlations with each other (Table S3). Dep was highly correlated with SWC, clay, silt, sand, TN, AP, SOM, pH, EC, altitude, and Tem ($|r|\geq 0.31$). High correlations were observed among most of these environmental factors ($|r|\geq 0.27$), except for the correlations of Dis and Pre with SWC, clay, silt, sand, TN, AP, SOM, pH, EC, Dep, and Tem, and the correlations of Tem with clay and SOM. Soil clay and silt were strongly correlated between each other and with sand, TN, and SOM ($|r|\geq 0.63$). Additionally, strong negative correlations were observed between SWC and Dep ($|r|\geq 0.88$) and among Dep, pH and EC ($|r|\geq 0.35$).

The CCA ordination showed the distribution of plant communities and their relationships with environmental factors (Fig. 4). Axes 1 and 2 of CCA accounted for 20.68% of the total variation and 54.77% of the fitted variance. Axis 1 of CCA explained 13.36% of the total variation (35.38% of the fitted variance), while axis 2 explained 7.32% of the total variation (19.39% of the fitted variance). Environmental factors significantly affected the composition of desert plant communities ($P<0.01$). Marginal effects indicated that all environmental factors, except Pre, were important for explaining the variation in vegetation patterns ($P<0.05$), and that most of this variation was explained by Dep, altitude, SWC, and Tem (Table 2). However, conditional effects were important for only 7 factors for explaining the variation in vegetation patterns ($P<0.05$; Table 2). These factors included Dep (11.70%), Dis (4.10%), EC (3.90%), silt (3.20%), altitude (2.80%), Tem (2.70%), and AP (2.20%). Overall, Dep, Dis, and EC explained most of the variability in vegetation patterns. In addition, no difference was observed between the marginal and conditional effects of Dis, indicating that the variance in Dis was not explained by Dep or EC. Conversely, SWC was highly correlated with Dep, which concealed the contribution of SWC to the interpretation of vegetation distribution variability (Table 2). These results were consistent with the results of Pearson's correlation analysis, indicating that Dep was closely associated with SWC. These relationships among environmental factors were also reflected in the CCA ordination (Fig. 4).
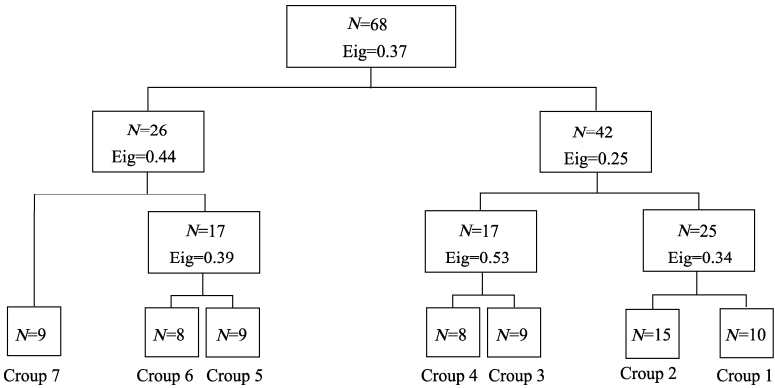

Fig. 2 Dendrogram showing the two-way indicator species analysis (TWINSPAN) classification of 68 plots. Eig, eigenvalue.

Table 1 Characteristics of the identified desert plant communities

Group	Community type	Habitat	C	H'	J_{sw}	D	Dominant species
1	Typical fruticous desert	Semi-fixed dune	0.35±0.07[ab]	1.19±0.22[bc]	0.48±0.09[b]	8.01±1.29[ab]	*Nit, Pha, Ags*
2	Desert shrub	Mobile dune	0.30±0.10[b]	1.37±0.33[b]	0.51±0.12[b]	9.27±3.44[a]	*Cal, Hal, Ags*
3	*Artemisia* desert	Semi-fixed dune	0.22±0.06[b]	1.69±0.26[a]	0.64±0.10[a]	6.44±1.15[b]	*Nit, Hal, Ara*
4	Dwarf tree desert	Fixed dune	0.23±0.07[b]	1.68±0.24[a]	0.62±0.09[ab]	7.21±0.78[b]	*Hal, Nit, Lia*
5	Halophyte bush vegetation	Fixed dune	0.28±0.09[b]	1.46±0.21[ab]	0.53±0.08[b]	8.48±1.22[ab]	*Tar, Res, Nit*
6	Salt semi-shrub	Saline land	0.24±0.08[b]	1.61±0.20[ab]	0.61±0.08[ab]	7.69±0.51[ab]	*Kaf, Lyr, Nit*
7	Saline meadow	Dry lake	0.42±0.10[a]	0.99±0.25[c]	0.51±0.13[b]	5.73±1.78[b]	*Nit, Pha, Sac*

Note: *C*, Simpson dominance index; *H'*, Shannon-Wiener diversity index; *J$_{sw}$*, Pielou evenness index; *D*, Margalef richness index; *Nit, Nitraria tangutorum*; *Pha, Phragmites australis*; *Ags, Agriophyllum squarrosum*; *Cal, Calligonum mongolicum*; *Hal, Haloxylon ammodendron*; *Ara, Artemisia salsoloides*; *Lia, Limonium aureum*; *Tar, Tamarix ramosissima*; *Res, Reaumuria songarica*; *Kaf, Kalidium foliatum*; *Lyr, Lycium ruthenicum*; *Sac, Salsola collina*. Mean±SD. Different lowercase letters indicate significant differences in the same column at *P*<0.05 level.
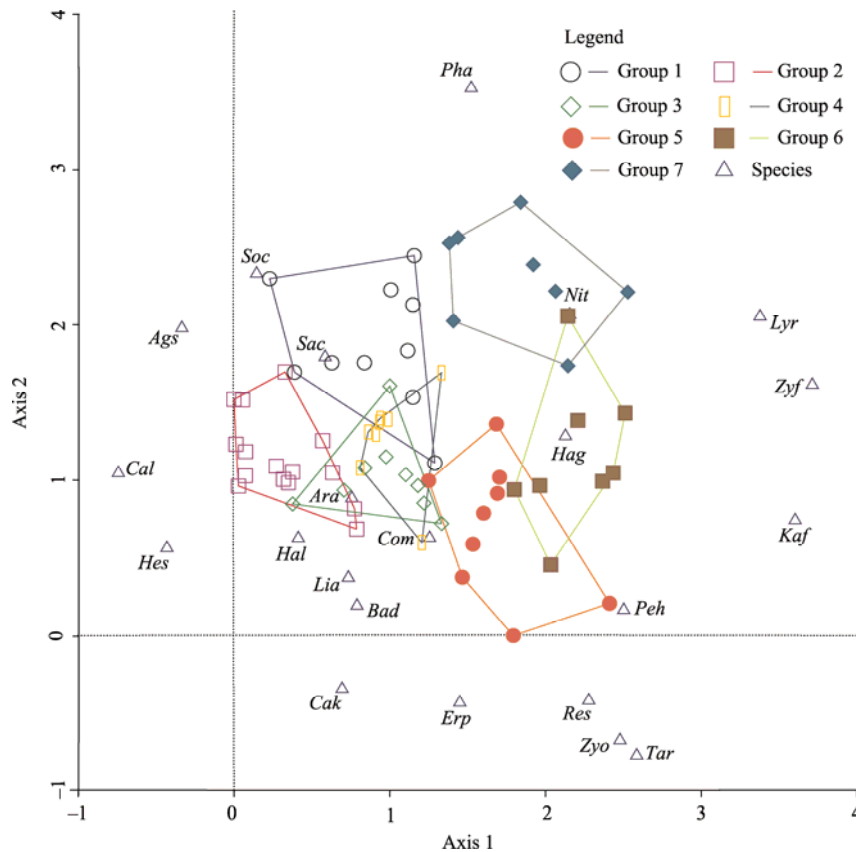
Fig. 3 Two-dimensional DCA (detrended correspondence analysis) ordination of 68 plots (7 community groups clustered by TWINSPAN) and dominant plant species. *Hal, Haloxylon ammodendron*; *Cal, Calligonum mongolicum*; *Nit, Nitraria tangutorum*; *Bad, Bassia dasyphylla*; *Hag, Halogeton glomeratus*; *Sac, Salsola collina*; *Ags, Agriophyllum squarrosum*; *Kaf, Kalidium foliatum*; *Com, Corispermum patelliforme*; *Zyf, Zygophyllum fabago*; *Zyo, Zygophyllum xanthoxylon*; *Hes, Hedysarum scoparium*; *Peh, Peganum harmala*; *Pha, Phragmites australis*; *Erp, Eragrostis pilosa*; *Hes, Hedysarum scoparium*; *Cak, Caragana korshinskii*; *Tar, Tamarix ramosissima*; *Res, Reaumuria songarica*; *Ara, Artemisia salsoloides*; *Lia, Limonium aureum*; *Lyr, Lycium ruthenicum*.

The results of CCA ordination indicated Dep, Dis, and EC as the main factors that explain the distribution patterns of desert vegetation in the Minqin ODE. Most vegetation species showed a clear distribution along the environmental gradients (Fig. 4). The first axis of CCA represented a strong groundwater gradient from 7.76 to 22.51 m, while the second axis indicated the gradient of soil properties along the ecotone. Desert shrub (*C. mongolicum*+*H. ammodendron*-*A. squarrosum*), typical fruticous desert (*N. tangutorum*-*P. australis*+*A. squarrosum*), and dwarf tree desert (*H. ammodendron*+*N. tangutorum*+*L. aureum*) communities were found inhabiting the edge of the oasis with high groundwater levels. *Artemisia* desert (*N. tangutorum*+*H. ammodendron*+*A. salsoloides*) and halophyte bush vegetation (*N. tangutorum*+*R. songarica*+*T. ramosissima*) communities were located in regions with medium groundwater levels and semi-fixed sand dunes. Salt semi-shrub (*K. foliatum*+*N. tangutorum*+*L. ruthenicum*) and saline meadow (*N. tangutorum*-*P. australis*-*S. collina*) communities were distributed in regions with low groundwater levels and fixed sand dunes in the Huqu.

The CCA ordination between dominant species and environmental factors revealed that the distribution of plant species varied with environmental factors (Fig. 5). *A. squarrosum* and *C. mongolicum* were present in regions with both high sand content (92.37% (±6.04%)) and high pH value (8.35 (±0.31)). *L. ruthenicum*, *Zygophyllum fabago*, and *K. foliatum* showed strong correlations with SWC (10.61% (±3.68%)) and EC (606.07 (±411.11)). *Caragana korshinskii*, *R. songarica*, and *Eragrostis pilosa* were associated with high clay content (6.43% (±3.12%)). *P.

australis was mainly distributed in the artificial water flood area of the Qingtu Lake with high SWC (12.25% (±2.30%)).
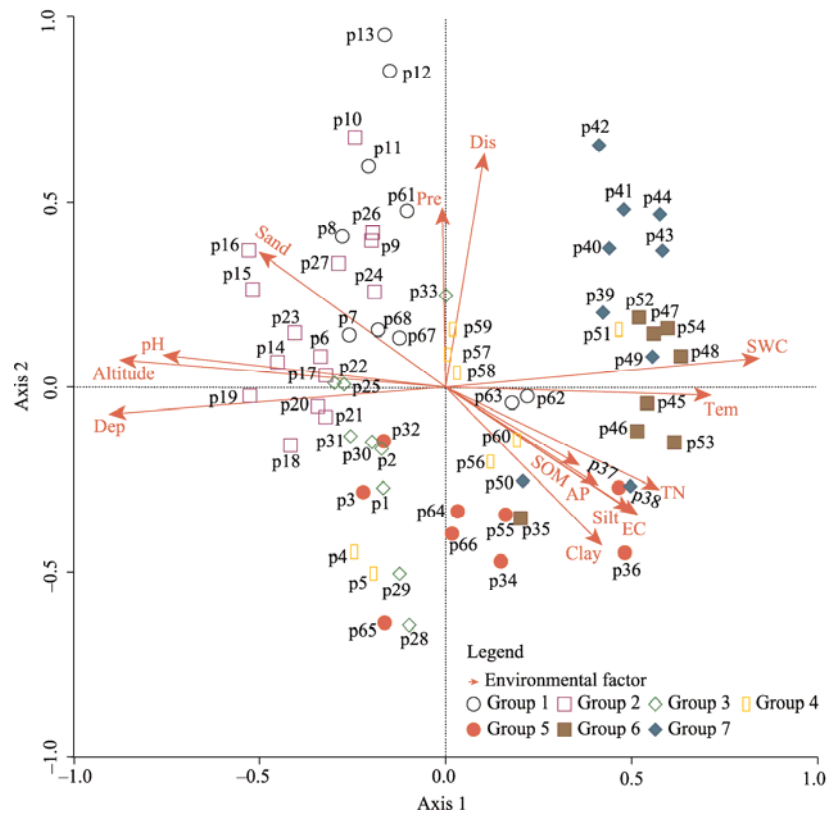
Fig. 4 CCA (canonical correspondence analysis) ordination of 68 plots (7 community groups clustered by TWINSPAN) and 14 environmental factors. The arrow indicates environmental factor, and the direction and length of arrow indicate the relationship of environmental factor with ordination axes. SWC, soil water content; Dep, depth of groundwater; Dis, distance between plot and oasis; Pre, mean annual precipitation; Tem, annual mean temperature; TN, total nitrogen; SOM, soil organic matter; AP, available phosphorus; EC, electrical conductivity.

4   Discussion

Sparse vegetation in desert ecosystems usually consists of shrub and herbaceous layers. The shrub layer comprises xeric, halophilic, and super-xeric species. Annuals and perennials are the main constituents of herbaceous layer, which grows with fluctuations in precipitation. In the Minqin ODE, shrubs are the constructive or dominant species of desert communities and play a significant role in maintaining species diversity. The artificial species *H. ammodendron* is distributed at the edge of oasis, while the natural species *N. tangutorum* is found in desert areas (Chen et al., 2007). Species resistance and interspecific relationship determine the community composition (Miriti, 2007). The most effective method to combat desertification is the establishment of sand-binding vegetation, which creates favorable conditions for colonization by many herbaceous species (Li et al., 2004). *H. ammodendron* plantations on mobile sand dunes in the Minqin ODE also promote the diversity of herbaceous vegetation (Fan et al., 2016). In this study, we quantitatively classified the sand-fixing vegetation into 7 plant community types, indicating the succession trend of desert vegetation. Desert perennials are considered as soil indicators in eastern Arabia on the basis of plant-soil relationships (Böer and Sargeant, 1998). The environmental indicator species can be used to determine soil chemical characteristics, especially in saline habitats (Angiolini et al., 2013). In this study, the distribution of *A. squarrosum* and *C. mongolicum* indicated the lowest SWC and the largest soil particle size, while that of *K. foliatum* and *L. ruthenicum* indicated the highest salinity and water levels and the finest soil texture.

Table 2 Marginal and conditional effects of environmental factors on plant communities

Environmental factor	General model			
	Marginal effects		Conditional effects	
	Variance explained (%)	Pseudo-F	Variance explained (%)	Pseudo-F
Dep	11.70	8.70[**]	11.70	8.70[**]
Altitude	11.40	8.50[**]	2.80	2.40[**]
SWC	10.30	7.50[**]	1.40	1.20[ns]
Tem	8.70	6.30[**]	2.70	2.30[**]
pH	8.30	6.00[**]	1.00	0.90[ns]
TN	5.80	4.10[**]	0.60	0.50[ns]
EC	5.60	3.90[**]	3.90	3.10[**]
AP	5.50	3.90[*]	2.20	1.90[*]
Silt	5.40	3.80[**]	3.20	2.60[**]
Sand	5.30	3.70[**]	—	—
Clay	4.60	3.20[**]	1.80	1.60[ns]
Dis	4.20	2.90[**]	4.10	3.20[**]
SOM	3.30	2.20[*]	1.00	0.90[ns]
Pre	2.50	1.70[ns]	1.30	1.10[ns]

Note: Dep, depth of groundwater; SWC, soil water content; Tem, annual mean temperature; TN, total nitrogen; EC, electrical conductivity; AP, available phosphorus; Dis, distance between plot and oasis; SOM, soil organic matter; Pre, annual mean precipitation. [ns], non-significant; [*], significance at $P<0.05$ level; [**], significance at $P<0.01$ level; —, no data.
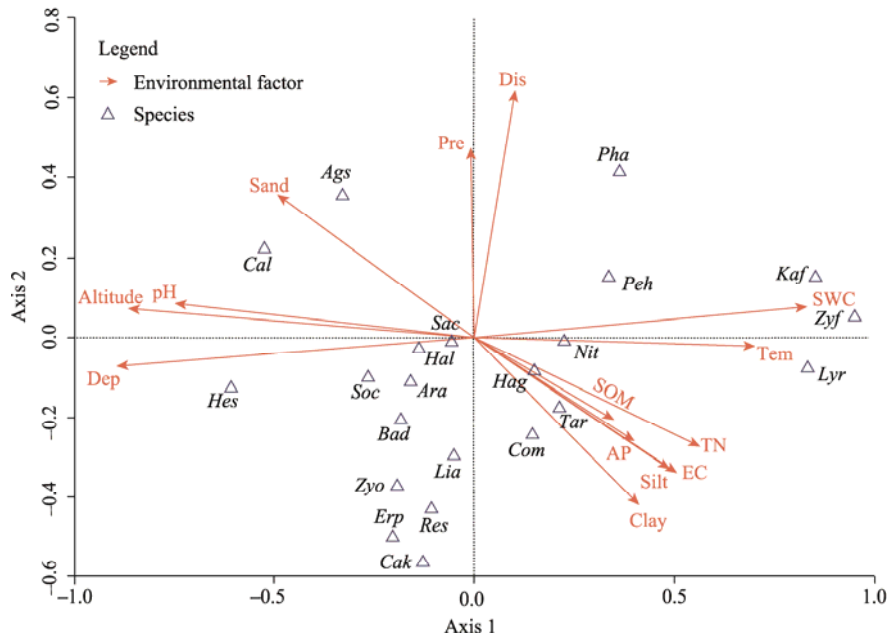

Fig. 5 CCA ordination of dominant species in the plant communities and environmental factors. The arrow indicates environmental factor, and the direction and length of arrow indicate the relationship of environmental factor with ordination axes. Abbreviations are the same as those in Figures 3 and 4.

Water is a deciding factor for the survival and development of desert plants. Groundwater is not only an important source of moisture for desert plants in dry seasons but also a determinant of the depth of the plant root system (Fan, 2015). It can affect the ecosystem function by changing vegetation structure. The heterogeneity of groundwater quality leads to niche differentiation among plant communities in the lower reaches of the Heihe River Basin (Zhu et al., 2014). In this study, CCA ordination showed that groundwater is a dominant environmental factor influencing the distribution of desert plants in the Minqin ODE. Changes in groundwater level in Baqu and

Quanshanqu were significantly higher than those in Huqu, with an average reduction of 0.64, 0.93, and 0.41 m, respectively, in 2008 (Chen and Feng, 2013). In the direction of groundwater flow (Baqu→Quanshanqu→Huqu), Mg^{2+}, the main component of cation, was gradually replaced by Na^+; SO_4^{2-} was consistently the dominant anion, whereas the proportion of Cl^- was gradually increased (Li et al., 2017). With the changes in groundwater level and quality, vegetation also changed from xerophytic to halophytic species. The ecological water conveyance project of the Qingtu Lake was implemented in 2010, which increased groundwater level. Because of improvement in hydrological conditions, the population of *N. tangutorum* declined gradually in the area surrounding the artificial lake in the dry lake basin, whereas the population of *P. australis* expanded over a large area.

Water uptake patterns of desert riparian plants vary with the depth of groundwater (Chen et al., 2016). *C. mongolicum*, *N. tangutorum*, and *T. ramosissima* mainly absorb soil water and groundwater in different periods of the growing season (Wu et al., 2014; Zhu et al., 2015; Ji et al., 2016). The optimum depth of groundwater for the increases in the height and cover of *N. tangutorum* ranges from 1.00 to 9.00 m and from 2.00 to 7.50 m, respectively, in the northeast region of the Ulan Buh Desert (Li et al., 2011). Woody plants have a deep root system and can absorb groundwater from the depth of 10.00 m or more. Wetland and riparian vegetation are more sensitive to groundwater depth (Le et al., 1999). Groundwater also influences the water physiology of *Populus euphoretic* (Chen et al., 2011) and improves the rainwater utilization efficiency of groundwater-dependent ecosystems in arid regions (Liu et al., 2017). Groundwater table at depths of 2.00–4.00 m is suitable for plant growth, as groundwater can prevent soil salinization within this range (Cui and Shao, 2005). When the groundwater level is below the maximum root depth, the vegetation cover is low and sensitive to changes in precipitation (Elmore et al., 2006). Young *H. ammodendron* plants mostly absorb soil water replenished by rainfall, whereas old *H. ammodendron* plants with a deep root system can access water from a greater depth (Zhou et al., 2017). Groundwater directly affects community composition through controlling water use by deep-rooted shrubs or perennial herbs, while indirectly influences vegetation distribution through soil salinization. Because of small spatial differences in precipitation distribution over the study area, the influence of rainfall on species composition of vegetation communities was not significant.

Landform constrains the vegetation type and dynamic changes in transgressive dune fields (Hesp et al., 2011). The distribution of sand-fixing pioneer plants is closely associated with soil moisture (Alamusa et al., 2017). The species composition of *H. ammodendron* plantation varies with the degree of sand dune fixation (Liu et al., 2014). Compared with tall dunes, flat and low fixed dunes can improve the diversity of herbaceous plants and the stability of ecosystems (Tao et al., 2017). Aeolian geomorphic process is an important factor affecting the distribution desert plants and other factors control the growth stages of plants and vegetation distribution by changing soil conditions (Szczuciński, 2012; Hernández-Cordero et al., 2015; Tang et al., 2016). From desert to oasis, the frequency of sand-laden wind, drift potential, and sand transport decreases while the roughness of surface increases (Zhang et al., 2017). The difference in dynamic aeolian conditions between oasis and desert shapes the dune microtopography, which restricts the distribution of desert plants. In this study, the Dis variable reflected the influence of topography on the species composition of desert plant communities.

The effect of soil factors on vegetation community structure is scale-dependent (Pan et al., 1998). In coastal dune environment, the distance from the coastline controls the vegetation distribution of coastal dunes by influencing soil proporties (Hwang et al., 2016). Variation in SOM along the oasis-desert gradient is obvious and closely related to the growth dynamics of annual plants (Chen et al., 2007). Soil surface sediment, $CaCO_3$, soil saturation, pH, and SOM are major drivers for the succession of coastal desert vegetation (Abd el-Ghani and Amer, 2003). The underlying soil processes of vegetation succession are acidification and the organic matter accumulation in Dutch wet dune is slack (Sýkora et al., 2004). Soil organic carbon, TN, and EC are highly correlated with community characteristics in the southern Mu Us Sandy Land (Xie et al., 2015). Soil moisture, salinity, and texture restrict the distribution of plant species in the lower reaches of the Heihe River

(Zhao et al., 2017). This study identified EC as the main soil factor affecting the distribution of desert vegetation. Because of differences in soil salinity, *C. mongolicum* was distributed only in the sandy desert habitat of Baqu, while *K. foliatum* and *L. ruthenicum* were found only in the saline habitat of Huqu.

Groundwater, Dis, and EC restrict each other and jointly determine the distribution pattern of desert vegetation on different scales. Additionally, Dis affects the groundwater depth, as a result of intensive irrigation of oasis (Wang and Zhao, 2015). Soil salinity in the study region is subject to groundwater salinity and vegetation cover (Qian et al., 2017). EC is an important indicator of soil salinization; therefore, groundwater affects soil EC. Soil pH, water pH, and EC are the main limiting factors affecting vegetation distribution in the hot, arid sub-tropical monsoon regions (Zereen and Sardar, 2015). In the Great Basin, groundwater depth and microtopography jointly affect the species distribution of desert vegetation (Mata-González et al., 2012). Thus, it can be concluded that the distribution and succession of vegetation are the outcomes of complex interactions among various environmental factors.

5   Conclusions

Vegetation in the Minqin ODE was composed of 28 plant species belonging to 27 genera in 8 families. TWINSPAN classification divided the desert vegetation into 7 community types. The species distribution of community types corresponded to their unique habitat characteristics. Results of CCA ordination indicated that groundwater was the most significant environmental factor affecting species composition, while Dis and EC were the second most important factors. Our results suggest that optimizing the utilization of groundwater in oases is the key to controlling the degradation of desert vegetation. In the future, plant sand-fixation projects should focus on the favorable topographic conditions of sand dunes, and more attention should be given to the limiting factors of soil salinity when selecting the tree species for afforestation. Multivariate analysis on desert vegetation in the Minqin ODE confirms the community types and driving environmental factors on the species distribution patterns. The results could further be applied for the rehabilitation of desert vegetation in arid and semi-arid regions in northwestern China as well as in other similar regions in the world.

Acknowledgements

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Appendix

Table S1 Species composition in the study area

Species	Family	Life form	Dominance index (%)
Haloxylon ammodendron	Chenopodiaceae	S	2.055
Bassia dasyphylla	Chenopodiaceae	AH	0.307
Halogeton glomeratus	Chenopodiaceae	AH	0.109
Salsola collina	Chenopodiaceae	AH	0.186
Agriophyllum squarrosum	Chenopodiaceae	AH	0.862
Kalidium foliatum	Chenopodiaceae	S	0.078
Corispermum patelliforme	Chenopodiaceae	AH	0.016
Nitraria tangutorum	Zygophyllaceae	S	4.726
Sarcozygium xanthoxylon	Zygophyllaceae	S	0.001
Tribulus terrester	Zygophyllaceae	AH	0.000
Zygophyllum fabago	Zygophyllaceae	PH	0.012
Peganum harmala	Zygophyllaceae	PH	0.000
Phragmites australis	Gramineae	PH	0.739
Stipa glareosa	Gramineae	PH	0.005
Chloris virgata	Gramineae	AH	0.000
Eragrostis pilosa	Gramineae	AH	0.027
Hedysarum scoparium	Leguminosae	S	0.001
Lespedeza potaninii	Leguminosae	S	0.000
Sophora alopecuroides	Leguminosae	PH	0.001
Caragana korshinskii	Leguminosae	S	0.001
Tamarix ramosissima	Tamaricaceae	S	0.186
Reaumuria songarica	Tamaricaceae	S	0.066
Artemisia salsoloides	Compositae	S	0.228
Artemisia frigida	Compositae	PH	0.001
Karelinia caspia	Compositae	PH	0.000
Calligonum mongolicum	Polygonaceae	S	0.783
Limonium aureum	Polygonaceae	PH	0.055
Lycium ruthenicum	Solanaceae	S	0.032

Note: S, shrub; AH, annual herb; PH, perennial herb.

Table S2 Statistics of environmental factors for the 7 plant community groups clustered by TWINSPAN

Environmental factor	Group 1	Group 2	Group 3	Group 4	Group 5	Group 6	Group 7
SWC	4.36±2.17^c	2.65±1.08^c	2.79±1.66^c	5.26±4.70^{bc}	7.26±3.73^b	10.61±3.68^a	12.25±2.30^a
Clay	2.78±2.27^{bc}	1.81±0.98^c	3.76±1.68^{abc}	4.64±3.62^{ab}	6.43±3.12^a	6.44±3.71^a	5.66±5.04^{ab}
Silt	10.97±12.06^{bc}	5.82±5.07^c	11.51±6.14^{bc}	16.89±13.13^{abc}	23.37±12.94^{ab}	27.38±16.11^a	21.83±17.77^{ab}
Sand	86.25±14.31^{ab}	92.37±6.04^a	84.73±7.74^{ab}	78.47±16.67^{abc}	70.20±15.95^{bc}	66.18±19.64^c	72.51±22.56^{bc}
TN	0.010±0.005^c	0.007±0.003^c	0.012±0.004^{bc}	0.015±0.010^{bc}	0.020±0.006^{ab}	0.026±0.010^a	0.024±0.017^a
AP	0.99±0.29^{bc}	0.81±0.13^c	0.75±0.28^c	1.16±0.25^{ab}	1.37±0.23^a	1.08±0.31^b	1.18±0.25^{ab}
SOM	0.27±0.17^c	0.21±0.07^c	0.28±0.09^c	0.34±0.23^{bc}	0.53±0.15^{bc}	1.02±1.26^a	0.78±0.52^{ab}
pH	8.00±0.30^a	8.35±0.31^a	8.14±0.55^a	7.54±0.42^b	7.61±0.18^b	7.15±0.37^{bc}	7.46±0.33^{bc}
EC	336.17±405.57^b	128.95±45.38^b	518.24±389.82^{ab}	288.99±198.72^b	783.17±320.98^a	606.07±411.11^{ab}	597.35±316.43^{ab}
Dep	19.73±2.20^a	22.23±1.67^a	22.51±1.83^a	16.11±5.20^b	15.36±5.35^c	6.78±5.38^c	7.76±1.27^c
Dis	4.20±1.46^a	2.57±1.62^{bc}	1.94±1.18^{bc}	2.25±0.80^c	1.25±1.00^c	2.81±1.75^b	2.94±0.95^b
Altitude	1344.70±28.21^b	1389.00±14.73^a	1362.02±12.10^b	1323.25±29.99^c	1324.56±24.85^c	1308.38±14.31^{cd}	1302.78±3.67^d
Pre	140.72±13.57^b	141.41±13.46^{ab}	131.72±1.51^b	135.88±2.70^b	133.13±3.21^b	135.23±3.77^b	146.79±14.57^a
Tem	6.48±1.02^b	5.52±0.00^c	5.53±0.05^c	6.95±0.84^{ab}	6.92±0.83^{ab}	7.01±0.61^{ab}	7.18±0.00^a

Note: SWC, soil water content; TN, total nitrogen; AP, available phosphorus; SOM, soil organic matter; EC, electrical conductivity; Dep, depth of groundwater; Dis, distance between plot and oasis; Pre, average annual precipitation; Tem, annual average temperature. Mean±SD. Different lowercase letters denote significant differences in the same row at P<0.05 level.

Table S3 Correlation coefficients among environmental factors

Environmental factor	SWC	Clay	Silt	Sand	TN	AP	SOM	pH	EC	Dep	Dis	Altitude	Pre	Tem
SWC	1.000													
Clay	0.596**	1.000												
Silt	0.631**	0.955**	1.000											
Sand	-0.629**	-0.971**	-0.998**	1.000										
TN	0.711**	0.824	0.810**	-0.818**	1.000									
AP	0.450**	0.341**	0.339**	-0.342**	0.387**	1.000								
SOM	0.466**	0.673**	0.633**	-0.646**	0.593**	0.273*	1.000							
pH	-0.669**	-0.497**	-0.539**	0.535**	-0.568**	-0.460**	-0.373**	1.000						
EC	-0.471**	0.515**	0.554**	-0.551**	0.362**	0.355**	0.299*	-0.537**	1.000					
Dep	-0.884**	-0.408**	-0.467**	0.458**	-0.645**	-0.445**	-0.313**	0.748**	-0.354**	1.000				
Dis	0.107	0.467	0.174	-0.159	0.010	-0.048	0.143	0.008	-0.105	-0.017	1.000			
Altitude	-0.739**	-0.379**	-0.433**	0.425**	-0.527**	-0.526**	-0.295*	0.728**	-0.473**	0.810**	0.007	1.000		
Pre	0.032	-0.163	-0.129	0.137	-0.088	-0.043	-0.091	0.093	-0.156	-0.065	0.183	0.132	1.000	
Tem	0.610**	0.236	0.310*	-0.298*	0.429**	0.578**	0.152	-0.643**	0.336**	-0.749**	-0.119	-0.900**	-0.072	1.000

Note: * means that correlation is significant at P<0.05 level, and ** means that correlation is significant at P<0.01 level.